

GEOMORPHIC LANDFORMS AND PLANT COMMUNITY STRUCTURE AND DOMINANCE IN THE CENTRAL DESERT REGION OF BAJA CALIFORNIA, MÉXICO

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ABSTRACT

Geomorphic gradients of landforms and associated soil catenas in the Central Desert region of Baja California produce complex but repeatable patterns of plant community distribution and a diversity of plant functional groups distributed unequally over the gradient. We measured plant diversity and made three assessments of plant dominance in six plant communities associated with a gradient of geomorphic landforms. Dominance was assessed by plant cover, aboveground biomass, and aboveground water mass held by vegetation. Perennial plant cover was highest on northeast-facing rocky pediment slopes (54.6%) and lower bajada slopes (45.7%), and lowest on creosote bush flats (19.2%). The highest aboveground biomass of any community (25.07 t ha⁻¹) was present in wash woodlands heavily dominated by *Prosopis glandulosa*. This was more than ten times the biomass present in the creosote bush flats. The highest aboveground water mass contained in vegetation was present on the northeast- and southwest-facing rocky pediment slopes which each held more than 30.0 t H₂O ha⁻¹. This water mass was heavily contained in just two species of arborescent stem succulents, *Pachycormus discolor* and *Fouquieria columnaris*, neither of which utilizes crassulacean acid metabolism (CAM). High amounts of standing water mass on upper and lower bajada slopes were held by the arborescent cactus *Pachycereus pringlei*. The changing pattern of relative dominance of plant functional groups across this gradient of desert landforms reflects the morphological and ecophysiological traits associated with each group, and indicates strong assembly rules of community composition.

Key Words: Baja California, bajada, Central Desert, plant functional group, soil catena, Sonoran Desert, stem succulent.

The Central Desert region of Baja California presents one of the iconic desert regions of the world with its high species diversity and remarkable range of plant functional groups ranging from tiny annuals to some of the tallest and most massive desert plants in the world (Wiggins 1980; Peinado et al. 2005; González-Abraham et al. 2010; Rebman and Roberts 2012; Wehncke et al. 2012). Charismatic and/or unusual plant species common in this region include *Fouquieria columnaris* (Kellogg) Kellogg ex Curran (Fouquieriaceae) and *Pachycereus pringlei* (S. Watson) Britton & Rose (Cactaceae) that can reach 20 m or more in height, large succulents such as *Lophocereus schottii* (Engelm.) Britton & Rose, *Stenocereus gummosus* (Engelm.) A. Gibson &

K.E. Horak (Cactaceae), and *Agave shawii* Engelm. (Agavaceae), the elephant trees *Pachycormus discolor* (Benth.) Coville (Anacardiaceae), *Bursera microphylla* A. Gray, and *B. hindsiana* (Benth.) Engl. (Burseraceae), and the large evergreen shrub *Viscainoa geniculata* (Kellogg) Greene (Zygophyllaceae).

Despite its relatively pristine condition and easy access from southern California, remarkably little quantitative research has taken place in the Central Desert region. The most complete vegetation description of the Central Desert remains that of Forrest Shreve based on surveys carried out on horseback more than 70 years ago (Shreve and Wiggins 1964). The Central Desert largely lacks detailed analyses of its biodiversity

resources and only portions of its southern area enjoy protection as a biosphere reserve (Ortega and Arriaga 1991; Peinado et al. 2005).

Geomorphic and hydrologic processes in the Central Desert region, as in other warm desert regions of the southwestern United States and adjacent northwestern México, produce a characteristic gradient of landforms and associated soil catenas. In these sequences, steep rocky upland areas erode to rocky pediment slopes formed by irregular masses of erosional debris resting on the mountain parent material. Hydrologic runoff from the mountains is directed into narrow arroyos that channel intermittent water flow and associated sediments. As these confined arroyos leave the uplands and open widely onto alluvial fans, the change in channel morphology and flow velocity leads to debris flow with the deposition of large amounts of sediments. The coalescence of these fans into a wide alluvial apron forms a broad bajada across the slopes. Below the bajada the desert landscape changes to extensive plains in the broad basins, with occasional braided washes that meander across the basin and channel heavier runoff flows.

In a simple scenario where the history of sediment transport has been fluvial and relatively simple, bajadas exhibit a regular gradation of particle sorting with coarser particles deposited upslope and finer particles moving down to the lower portions of the bajada (Mabbutt 1977; MacMahon 1988). Under such conditions the coarser soils on the upper fan allow more rapid infiltration of water into the soil during rain or intermittent surface flow and a less tenacious hold on this water (higher soil water potentials) than on finer textured soils low on the fan (Yang and Lowe 1956). These lower bajada slopes are characterized by rapid rates of runoff and thus low rates of moisture infiltration. In addition, the fine texture of soil particles of the lower bajadas and valley flats below promotes capillarity which draws moisture to the soil surface where it readily evaporates, further reducing soil moisture availability and decreasing soil water potential, as well as concentrating salts at the soil surface. These catenas of soil structure and texture have profound impacts on rates of soil water distribution and availability for plant growth.

Complicating this generalized pattern of predictable gradients of geomorphic surfaces is the reality of the complex depositional history that affects most bajadas. Many of these erosional features date back to the Pleistocene, with cyclic changes of depositional flows at millennial frequencies superimposed over Holocene patterns of complexity in depositional flows over decadal and longer intervals (Mabbutt 1977; McAuliffe 1994). Thus, complex variation in the spatial pattern of debris flows in geologic and historical time can have profound impacts on vegetation

structure (Burk and Dick-Peddie 1973; Stein and Ludwig 1979; McAuliffe 1991).

Differing morphological and ecophysiological traits associated with desert plant functional groups has been hypothesized to allow plants of differing functional groups to compete less with those in other groups than their own group for limiting soil water resource or other resources (Yeaton and Cody 1976; Bowers and Lowe 1986). Understanding the costs and benefits of these traits and their phylogenetic limitations can provide a useful approach to understanding how vegetation structure changes along environmental gradients (Westoby et al. 2002; Westoby and Wright 2006).

Our objectives in this study have been to add to knowledge of the Central Desert region by quantifying patterns of plant community composition, functional group distribution, and three measures of stand dominance in plant communities along a gradient of geomorphic surfaces in an area of unique biological and morphological plant diversity in the Central Desert southwest of Cataviña. Our three assessments of dominance included ground cover as a measure of spatial dominance, aboveground biomass as a measure of sustainable long-term net productivity, and aboveground water mass stored as a measure of potential buffering against drought. Beyond this, we hypothesized that plant functional groups will be differentially distributed across these geomorphic gradients, with water availability in shallow and deeper soil profiles as primary determining factors.

MATERIALS AND METHODS

Site Description

Our field site was located in the Central Desert region of Baja California southwest of Cataviña (29°44'N, 114°43'W). The site was situated 18 km south of Baja Highway 1 along a dirt road to La Bocana, whose junction was about 12 km west of Cataviña and 113 km southeast of El Rosario. We studied a gradient of geomorphic sites beginning with rocky pediments on the hilly slopes and moving down in elevation through an upper bajada, a wider lower bajada, extensive alluvial flats, and finally to a broad wash with braided channels across the valley bottom. Elevations ranged from about 680 m on the rocky pediment to about 480 m on the wash below.

The broad geological parent material of the area is granitic tonalite, a batholithic rock that weathers into sandy material. There were pre-batholithic schists as well on the pediment slopes that weathered into finer textured material. The broad wash consisted of Quaternary fluvial deposits overlain by young alluvium. Soils on

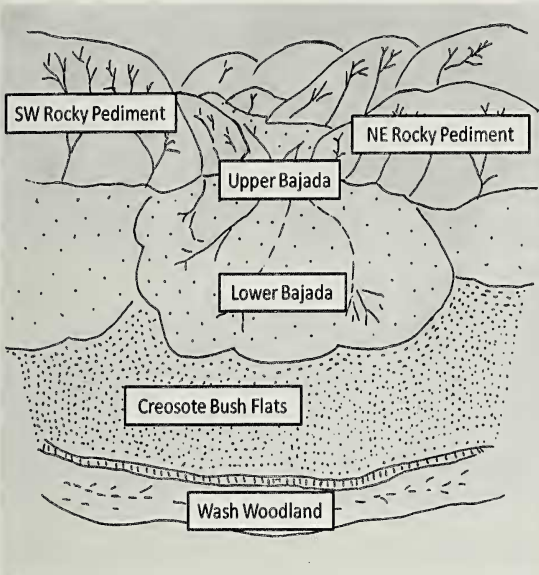


FIG. 1. Diagrammatic representation of the six geomorphic landforms sampled at the study site.

the rocky pediment slopes were sandy loams, while those on the bajada were a mixture of loamy sands and sandy loam. The broad alluvial flats below the bajada had extensive areas of loamy sand, and smaller distinctive areas of loam, as described in more detail below. The wash area exhibited coarse sandy soils.

Precipitation at Cataviña averages about 90 mm annually, with a distinct biseasonal pattern of rainfall. This mean amount, however, masks a high variance in both intra- and interannual rainfall across the Baja California peninsula (Bullock 2003).

Field Sampling

Field sampling and measurements were carried out on a series of three separate field expeditions over a period of two years. We sampled the aboveground cover of all species of woody, semi-woody and succulent perennials using non-biased placement of 50 m line transects in a series of 0.1 ha plots representing six distinctive geomorphic plant communities: 1) northeast-facing rocky pediment slopes (n = 8); 2) southwest-facing pediment slopes (n = 8); 3) upper bajada (n = 8); 4) lower bajada (n = 5); 5) alluvial flats (n = 8), and wash woodlands (n = 8) (Fig. 1). The two pediment slope facings reflect that present with the natural topography. Because these desert communities are inhomogeneous and our sample sizes are relatively small we chose to present our data for cover, as well as biomass and water mass as described below, as mean values and not calculating the large error bars around these means. We feel that these means reasonably

represent community characteristics, as defined in classic gradient studies of aridlands by Whittaker and Niering (1965, 1975). Nevertheless, our sample data for this gradient lacks rigorous statistical significance because of the natural inhomogeneity of desert habitats.

Each species sampled was characterized as representative of one of five plant functional groups with differing ecological strategies of leaf phenology and/or ecophysiology: 1) drought deciduous shrubs that lose their leaves under conditions of water stress; 2) xerophytic evergreen shrubs which maintain leaves throughout the year; 3) phreatophytic shrubs and trees with leaf loss in winter; 4) leaf and stem succulents that utilize crassulacean acid metabolism (CAM); and, 5) stem succulents (pachycauls) with drought deciduous leaves and which lack CAM photosynthesis (Bobich and North 2009).

Depending on canopy size, replicated volumes of 1/4 to 1/2 of representative canopy areas of each of the important shrub species were sampled, weighed, and oven-dried to provide data on aboveground dry weight biomass (kg ha^{-1} ; Ludwig et al. 1975) and water content per unit area ($\text{kg H}_2\text{O ha}^{-1}$). Estimates of the biomass and water content of minor subshrub species were made based on data for the most similar canopy type sampled for the common species. Estimates of the biomass and water content of large CAM succulents and stem succulents were made using subsampling techniques previously described (Nilsen et al. 1984). Biomass and water content of *Prosopis glandulosa* Torr. were measured using a series of biomass subsamples and measurements and extended using regression equations developed in previous studies with this species (Sharifi et al. 1985).

RESULTS

Species Richness and Plant Functional Groups

Field transects in the six geomorphic plant communities along our gradient of geomorphic habitats included 44 species of perennial plants. However, more than 100 species were identified along our gradient including species present but not sampled within our transects. The largest total number of species sampled occurred on the two pediment slopes, with 18 species on the southwest-facing slopes and 14 species on the northeast-facing slopes. Including all perennial species encountered in the 0.1 ha plots, these two pediment slopes had 41 and 31 species, respectively. Next in species richness was the wash woodland with 17 species sampled (Table 1). The other three communities had only slightly fewer species with 9–12 perennials sampled.

Of the 44 species encountered in our samples, two-thirds (29 species) were drought deciduous

TABLE 1. COVERAGE (% GROUND SURFACE) OF PERENNIAL PLANT SPECIES SAMPLED IN SIX GEOMORPHIC PLANT COMMUNITIES ALONG THE CATAVIÑA GRADIENT. Plant functional groups are DD = drought deciduous shrub or subshrub, WD = winter deciduous shrub or tree, E = evergreen shrub, CS = CAM succulent, and SS = non-CAM stem succulent (pachycaul).

	Functional group	NE rocky pediment	SW rocky pediment	Upper bajada	Lower bajada	Creosote bush flats	Wash woodland
<i>Acmispon glaber</i>	DD	19.6		0.4	20		
<i>Agave</i> cf. <i>cerulata</i>	CS	2.8	4		2.5	0.2	
<i>Ambrosia chenopodiifolia</i>	DD	3.4	0.05		7.2	0.4	
<i>Ambrosia dumosa</i>	DD		0.5			5.9	
<i>Ambrosia monogyra</i>	DD						<0.1
<i>Atriplex polycarpa</i>	E					0.03	2.2
<i>Bahiopsis deltoidea</i>	DD						0.05
<i>Bahiopsis laciniata</i>	DD	15.5			0.3		
<i>Croton californicus</i>							
<i>Cylindropuntia cholla</i>	CS		0.6	0.6			
<i>Cylindropuntia</i> sp.	CS	0.05			1.4	0.05	
<i>Encelia asperifolia</i>	DD			3.6	0.7	0.03	0.1
<i>Encelia farinosa</i>	DD		10				
<i>Ephedra californica</i>	E						1.1
<i>Eriogonum fasciculatum</i>	DD	4	0.05	0.5	0.3	0.3	
<i>Fagonia laevis</i>	DD		0.2				
<i>Fouquieria columnaris</i>	SS	0.4	1				
<i>Fouquieria splendens</i>	SS		1				
<i>Hibiscus denudatus</i>	DD		1.4				1.3
<i>Krameria bicolor</i>	DD		0.2			1.5	
<i>Krascheninnikovia lanata</i>	DD					0.1	
<i>Larrea tridentata</i>	E	0.2	0.6	10.5		9.9	0.2
<i>Lycium andersonii</i>	DD			1.8	11.3		
<i>Lycium</i> cf. <i>californicum</i>	DD	0.8					
<i>Lycium megacarpum</i>	DD						3.2
<i>Lycium</i> sp.	DD	0.5					
<i>Marina parryi</i>	DD		0.8				
<i>Mirabilis laevis</i>	DD	0.1		0.05	0.4		0.05
<i>Nicotiana trigonophylla</i>	DD						0.05
<i>Pachycereus pringlei</i>	CS			0.2	0.5		
<i>Pachycormus discolor</i>	SS	4.8	4.9				
<i>Peritoma arborea</i>	DD						0.05
<i>Peucephyllum schottii</i>	DD		0.8				
<i>Polygala desertorum</i>	DD	0.05	0.2				
<i>Prosopis glandulosa</i>	WD						25.2
<i>Psorothamnus spinosus</i>	WD						0.05
<i>Salazaria mexicana</i>	DD					0.03	
<i>Senecio</i> sp.	DD				0.6	0.1	
<i>Senegalia greggii</i>	WD						1
<i>Simmondsia chinensis</i>	E	2.4				0.5	
<i>Solanum hindsianum</i>	DD		1		0.5		0.05
<i>Sphaeralcea</i> sp.	DD						0.05
<i>Stillingia linearifolia</i>	DD		0.2	0.2		0.03	0.05
<i>Viscainoa geniculata</i>	E			7.6			
Total		54.6	27.5	25.4	45.7	19.2	34.8

shrubs and subshrubs (Table 1). There were five evergreen shrub species, three wash phreatophytes, four CAM succulents, and three non-CAM stem succulents (pachycauls).

Perennial Plant Cover

The highest cover of 54.6% for perennial plant species was present on the NE-facing pediment slopes (Fig. 2a; Fig. 3), with a large proportion of this due to two subshrub species – *Acmispon glaber* Brouillet (formerly *Lotus scoparius* [Torr.

& A. Gray] Ottley) and *Bahiopsis laciniata* (A. Gray) E. E. Schill. & Panero. Next in importance was the stem succulent *Pachycormus discolor* with 4.8% cover, followed by the semi-woody shrubs *Eriogonum fasciculatum* Benth. and *Ambrosia chenopodiifolia* (Benth.) W. W. Payne with 4.0 and 3.4% coverage, respectively.

The SW-facing pediment slopes had a mean cover of 27.5%, but with a markedly different species composition. The dominant species was *Encelia farinosa* A. Gray ex Torr. with 10.0% cover, followed by *Pachycormus discolor* with

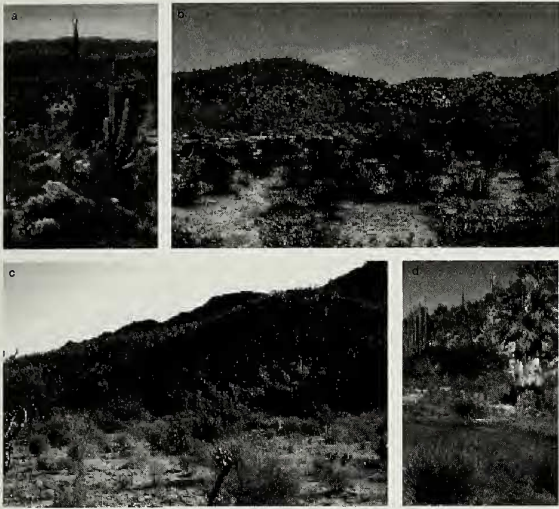


FIG. 2. Photographs of field site. a) northeast-facing pediment slope; b) creosote bush flats; c) upper bajada and southwest-facing pediment slope; and d) wash woodland with *Washingtonia robusta*.

4.9% cover. These two pediment sites were the only areas where *P. discolor* was present. Neither of the two dominants from the northeast-facing slopes, *Acmispon glaber* and *Bahiopsis laciniata* were present.

The upper bajadas slope had a mean cover by perennial plants of 25.4%, with *Larrea tridentata* (Sessé & Moc. ex DC.) Coville the dominant species with 10.5% cover. Next in dominance were *Viscainoa geniculata*, a large evergreen shrub in the Zygophyllaceae, with 7.6% cover, and *Encelia asperifolia* (S. F. Blake) Clark & Kyhos with 3.6% cover.

The lower bajadas differed significantly from the upper bajadas in species composition. The mean coverage was 45.7%, but neither *L. tridentata* nor *V. geniculata* was present. The dominant species was *Acmispon glaber* with 20.0% cover, followed by *Lycium andersonii* A. Gray with 11.3% cover and *Ambrosia chenopodiifolia* with 7.6%.

Creosote bush flats had a mean perennial plant cover of 19.2%. *Larrea tridentata* was the overall dominant in cover with a mean of 9.9%, followed by *Ambrosia dumosa* (A. Gray) W. W. Payne with 5.9% cover. Other perennial plant species with small but significant cover included *Krameria bicolor* S. Watson (1.5%) and *Simmondsia chinensis* (Link) C. K. Schneid., *Eriogonum fasciculatum*, *Ambrosia chenopodiifolia* and *Agave cf. cerulata* Trel., each with less than 1% cover.

The wash woodland community had a ground cover of 34.8%, largely due to the presence of a stand of *Prosopis glandulosa*, which had a mean cover of 25.2%. Ten of the 17 species sampled in the wash woodland samples occurred nowhere else on the transect (Table 1). These included

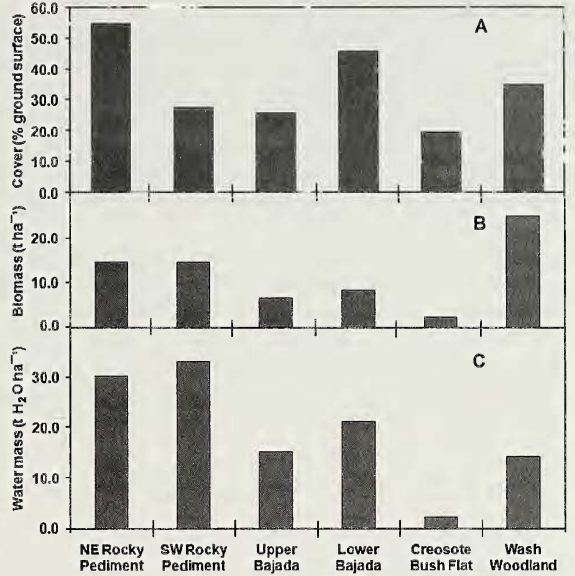


FIG. 3. Perennial plant cover (% of ground surface), aboveground biomass ($t\ ha^{-1}$), and aboveground water mass ($t\ H_2O\ ha^{-1}$) for each of the six geomorphic plant communities sampled.

woody legumes such as *Senegalia greggii* (A. Gray) Britton & Rose and *Psoralea spinosa* (A. Gray) Barneby, *Ephedra californica* S. Watson, *Peritoma arborea* (Nutt.) Iltis, *Lycium megacarpum* Wiggins, *Croton californicus* Müll. Arg., and *Bahiopsis deltoidea* (A. Gray) E. E. Schill. & Panero.

Perennial Plant Aboveground Biomass

Assessing plant community structure on the basis of aboveground dry weight biomass changed the relative ranks of communities. The highest stand biomass was present in the wash woodland community, with $25.07\ t\ ha^{-1}$ (Fig. 2d; Fig. 3). A single species, *Prosopis glandulosa*, provided about 90% of this biomass. Next in biomass with almost identical amounts were the NE-facing and SW-facing pediment slopes with 14.64 and $14.72\ t\ ha^{-1}$, respectively. More than 60% of the biomass on both of these slopes was provided by two stem succulent species, *Pachycornus discolor* and *Fouquieria columnaris*, with *Agave cf. cerulata* also providing significant biomass. The large ground coverage of *Acmispon glaber* (19.6%) on the NE-facing slopes provided only 4% of the community biomass. In contrast, the moderately large coverage of *Encelia farinosa* (10.0%) on the SW-facing slopes provided 9% of the community biomass.

Intermediate levels of stand biomass were found in the upper and lower bajada communities. The lower bajada slope had the higher biomass, with $8.50\ t\ ha^{-1}$. The largest relative component of

this biomass was contributed by *Lycium andersonii* with 39%, followed by *Pachycereus pringlei* (20%), *Agave* L. (18%), and *Acmispon glaber* (10%). The upper bajada slope had an above-ground biomass of 6.58 t ha⁻¹. The major coverage of *Viscainoa geniculata* on this slope provided 36% of this biomass, followed by *Larrea tridentata* (22%), *Pachycereus pringlei* (20%), and *Lycium andersonii* (8%).

The smallest amounts of stand biomass were measured in the creosote bush flats, with an aboveground biomass of 2.35 t ha⁻¹. *Larrea tridentata* and *A. dumosa* together accounted for 86% of the biomass, followed by *Agave* and *S. chinensis* with 5% of the community biomass each.

Water Content of Aboveground Biomass

A third measure of stand dominance is the amount of water held in aboveground tissues. For woody shrub species, the biomass values ranged from a high of 3.08 kg m⁻² of canopy for *Viscainoa geniculata* and 2.92 kg m⁻² for *Lycium andersonii* to lows of 0.53 kg m⁻² for *Eriogonum fasciculatum* var. *polifolium* (Benth.) Torr. & A. Gray and 0.63 kg m⁻² for *Bahiopsis laciniata*. The tissues of larger succulents, however, held more water per unit of coverage.

At a community level, plants on both the NE-facing and SW-facing pediment slopes held far more water in their aboveground tissues than that present in other communities (Fig. 2c; Fig. 3), due in large part to the presence of stem succulent and CAM succulent functional groups. The NE-facing slopes had a community water content of 30.32 t H₂O ha⁻¹, compared with a similar 33.23 t H₂O ha⁻¹ on the SW-facing slopes. These amounts produce a ratio 2.07 and 2.26 kg H₂O/kg biomass.

Just three succulent species combined to account for 91% and 93%, respectively; of the aboveground water content on these slopes. These were *Pachycormus discolor* (43% and 40%), *Fouquieria columnaris* (26% and 24%), and *Agave* cf. *cerulata* (22% and 29%). *Bahiopsis laciniata* held the highest relative water mass of any of the non-succulents on the NE-facing slopes, with just 3%. On the SW-facing slopes this position was held by *Encelia farinosa* with 4% relative water mass.

Intermediate levels of aboveground water content were found on the upper bajada slope (15.18 t H₂O ha⁻¹), lower bajada slope (21.31 t H₂O ha⁻¹), and in the wash woodland community (25.07 t H₂O ha⁻¹). The ratios of water content to biomass were 2.31 in the upper bajada community and 2.51 in the lower bajada community, values slightly higher than those on the pediment slopes above. The wash woodland community, however, had a water content to

biomass ratio of only 0.57, the lowest of any community along our transect.

The relatively high levels of water content on the upper and lower bajada slopes was due primarily to the presence of a large arborescent cactus, *Pachycereus pringlei*, which accounted for 69% and 49%, respectively, of the relative water content despite contributing less than 0.2% and 0.5% cover, respectively. On the upper bajada slope the next most important species for water content were the evergreen shrubs *Viscainoa geniculata* with a relative community water content of 15% and *Larrea tridentata* with 7%. On the lower bajada slope, a large coverage of *Agave* cf. *cerulata* provided 28% of the relative water content of the community, followed by *Lycium andersonii* with 16%.

In the wash woodland community, *Prosopis glandulosa* was the overwhelming dominant in accounting for aboveground water content in the community, holding 86% of the total. *Lycium megacarpum* was second in importance with just 7% of the community water content, followed by *Atriplex polycarpa* and *Ephedra californica* with just 2% each.

The creosote bush flats held very little water in aboveground tissue, with a community total of just 2.07 t H₂O ha⁻¹, only about 6–7% of the amount of water held by vegetation on the rocky pediment slopes. The largest amount of water was held by *L. tridentata* with 47% of the community total, followed by *Agave* cf. *cerulata* with 23% and *Ambrosia dumosa* with 19%.

DISCUSSION

The ecophysiological implications of the pattern of geomorphic gradients at our study site are strongly related to the linked characteristics of soil structure and water availability. Rocky pediment slopes, relatively poorly studied in the desert ecological literature, have shallow soils and provide only local points of enhanced water availability where fractures in the underlying bedrock surface or sediment accumulation can trap moisture. These are areas where succulent plants and shallow-rooted drought deciduous shrubs can best survive.

The upper bajada slopes are fed by concentrated water flow during intermittent rain events and the coarse soil texture allows for mosaics of water availability in the soil strata and thus a mix of plant growth forms and relative species diversity. In contrast, lower bajada slopes and the creosote bush flats below are generally considered to be more xeric sites because of the fine textured soil, which limits water infiltration and thus support lower plant diversity and abundance. Patterns such as this have been reported for several areas of the summer and biseasonal rainfall Sonoran Desert (Whittaker

TABLE 2. RELATIVE COVER (%), RELATIVE ABOVEGROUND BIOMASS (%), AND RELATIVE ABOVEGROUND WATER MASS (%) OF PLANT FUNCTIONAL GROUPS FOR EACH GEOMORPHIC PLANT COMMUNITY SAMPLED.

	Drought deciduous	Evergreen shrub	Winter deciduous	CAM succulent	Non-CAM stem succulent
Relative cover (%)					
NE rocky pediment	80.6	4.8	0	5.2	9.1
SW rocky pediment	56	2.2	0	16.7	25.1
Upper bajada	25.8	71.3	0	3.1	0
Lower bajada	90.4	0	0	9.6	0
Creosote bush flat	43.3	54.3	0	2.4	0
Wash woodland	14.5	10.1	75.6	0	0
Relative biomass (%)					
NE rocky pediment	19.6	4.3	0	12.1	64.2
SW rocky pediment	14.1	0.6	0	17.8	67.5
Upper bajada	15.4	57.1	0	27.5	0
Lower bajada	59.2	0	0	40.7	0
Creosote bush flat	32.4	62.2	0	5.4	0
Wash woodland	4.3	3.6	92.1	0	0
Relative water mass (%)					
NE rocky pediment	7	1.7	0	22.2	69.1
SW rocky pediment	4.5	0.2	0	30.1	65.2
Upper bajada	5.8	22.3	0	71.8	0
Lower bajada	18	2.8	0	79.1	0
Creosote bush flat	25.2	51.6	0	23.2	0
Wash woodland	7.3	4.2	88.5	0	0

and Niering 1965; Phillips and MacMahon 1978, Key et al. 1984, Bowers 1988; Parker 1991, 1995).

Excluding the wash woodland community, the ranges of aboveground biomass found in our study ranged from 2.35–14.72 t ha⁻¹. These compare well with biomass values of 3.92–13.10 t ha⁻¹ reported for three desert communities on the lower slopes of the Santa Catalina Mountains in Arizona (Whittaker and Niering 1975). Our wash woodland stand of *Prosopis glandulosa* has an aboveground biomass of 25.1 t ha⁻¹, which is similar to a biomass of 23 t ha⁻¹ measured in a *Prosopis* wash woodland in the Sonoran Desert of southern California (Sharifi et al. 1982). High aboveground biomass has also been described for open stands of *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth in northern Peru (Padrón and Navarro-Cerrillo 2007).

Perennial species in *Larrea/Lycium* shrublands of Rock Valley in the eastern Mojave Desert have an aboveground biomass of 1.04–1.32 t ha⁻¹ (Rundel and Gibson 1996), which is only about half of the values we measured for the *Larrea* flats at our Baja California site. The higher values at our site may reflect the longer growing season with a biseasonal rainfall regime. More mesic stands of *Larrea divaricata* Cav. and *L. cuneifolia* Cav. in the lowlands near Mendoza, Argentina, have been reported to have an aboveground biomass of 5.7–10.5 t ha⁻¹ (Martínez Carretero et al. 2007), and high density stands *Larrea tridentata* at the Jornada Range in New Mexico have an aboveground biomass of about 5.8 t ha⁻¹ (Barbour et al. 1977).

Our data demonstrate site specific spatial patterns of ecological dominance and codominance for the five plant functional groups treated. These patterns are shown in the absolute and relative cover, biomass, and water mass for each plant functional group along our gradient of communities (Table 2). Drought deciduous shrubs, which comprise the largest group of species in our study, form the overwhelming cover dominant on the NE-facing slopes, SW-facing slopes, and lower bajada, and are co-dominant on the creosote bush flats. With few exceptions, these are thought to be relatively short-lived opportunistic species (Miriti et al. 1998).

When viewed on the basis of aboveground biomass, however, the story is quite different. The relative biomass contribution of these drought deciduous species is small and dominates only on the lower bajada. In no community do they hold the largest proportion of biomass. These results are not surprising given that many of these drought deciduous shrubs have high rates of productivity but turn over their leaf biomass annually. Most drought deciduous species lack the amount of long-lived woody tissues present in the evergreen shrubs, with *Lycium* L. species as an exception.

Evergreen shrubs form the cover and biomass dominants on upper bajada slopes and the creosote bush flats, with values driven almost entirely by just two long-lived species of Zygophyllaceae. Only in the creosote bush flats is this relative dominance maintained in water mass,

and here because of an absence of any significant cover by CAM or stem succulents.

These two functional groups with succulent storage tissues take on a large role in stand biomass and water mass despite their low stand cover. High levels of aboveground tissue water in these succulents suggest that such storage can aid these species and promote longevity by buffering the effects of interannual variability of rainfall that characterizes their habitat. In relation to regional rainfall amounts, this storage capacity is low, representing no more than the equivalent of three mm of rainfall in even the stands with the highest aboveground water content in plant tissues. In relation to seasonal transpiration budgets, however, thus stored water may be highly significant in buffering succulent plant species from water stress.

Pachycormus discolor and *Fouquieria columnaris* had very low densities on the rocky pediment slopes but nevertheless were the dominants in both relative stand biomass and water mass for these communities. The drought-deciduous leaf tissue in both species allows them considerable flexibility in controlling water loss. These are clearly long-lived species that are episodically successful colonists on rocky slopes (Bashan et al. 2000, 2006). There are estimates that *F. columnaris* may live well over a century (Humphrey 1974), but its lifespan while long is less than that of *Pachycereus pringlei* (Bullock et al. 2005).

The presence of CAM in the cacti and agave combined with a low surface to volume ratio for the photosynthetic stems or leaves and thick cuticle to limit water loss all provide extremely high water use efficiency well beyond that of any of the plants lacking this metabolic system (Nobel 2003). It is tempting to lump CAM plants with succulent storage tissue into a single functional group with non-CAM stem succulent species as both are characterized by high tissue water content relative to the daily water use during the growing season. Certainly the water storage capacity at our site for large cacti such as *Pachycereus pringlei* and *Cylindropuntia cholla* (F.A.C. Weber) F.M. Knuth, with trunk water contents of 4.2 and 3.2 kg H₂O m⁻³ respectively, is matched by the stem succulent *Fouquieria columnaris* with a storage capacity of 3.6 kg H₂O m⁻³ (Nilsen et al. 1990). The stem succulent tree *Pachycormus discolor*, however, had a volumetric storage capacity of only 1.0 kg H₂O m⁻³, little more than the water content of woody tissues of *Prosopis glandulosa*, *Larrea tridentata*, or *Simmondsia chinensis* (Nilsen et al. 1990). However, *P. glandulosa* maintains a full leaf canopy through the hot summer months, while *P. discolor* is leafless for extended periods of months when water stress is present.

CAM succulent species had small but significant cover on all of the rocky pediment and

bajada communities but did not approach cover dominance in any of these. Similarly, they were proportionally more significant in relative stand biomass but again did not form the stand dominant functional group in any of these four communities. Their succulence, however, gave this group significant relative water mass in every community except the wash woodland, and a strong dominance in relative water mass in the two bajada communities where *Pachycereus pringlei* was present. Over its range, the long-lived *P. pringlei* exhibits differing patterns of abundance and population structure, with episodic conditions of establishment as a major determining factor (Bullock et al. 2005; Medel-Narvaez et al. 2006). The successful establishment of this species, and possibly other cacti, has been hypothesized to be linked to the presence of endophytic bacteria that aid in releasing available nutrients for seedling uptake from rocky substrates (Puentes et al. 2009).

In contrast to CAM succulents, the non-CAM stem succulents have drought deciduous leaves as their primary photosynthetic organs and fix carbon during the daylight hours using Rubisco. Thus, despite a relatively high water storage capacity these species lack the water use efficiency of the CAM succulents. With a relatively small total leaf area, *Fouquieria columnaris* has a water content in its succulent trunk equivalent to 67 days of water use in the growing season were all of this water available (Nilsen et al. 1990). *Pachycormus discolor*, which likewise has a fairly small total leaf area but lower trunk water content, holds water equivalent to 22 days of transpiration. This buffering capacity can be contrasted to that of *Prosopis glandulosa* whose trunk water storage is continuously recharged with its phreatophytic roots, and whose tissues hold an equivalent of only 1.6 days of water use (Nilsen et al. 1990). Drought deciduous shrubs have little buffering capacity with stored water, and thus can only photosynthesize with concomitant water loss through transpiration when the roots can access soil moisture.

Winter deciduous phreatophytes such *Prosopis glandulosa*, *Senegalia greggii*, and the functionally leafless *Psoralea argophylla* were all limited along our gradient to the wash woodland community where their roots can tap lenses of groundwater (Rundel et al. 1982; Nilsen et al. 1984, 1989). The degree to which these species require permanent groundwater pools depends somewhat on the amount and seasonality of their rainfall. The low but bimodal rainfall of the study area largely restricts these species to wash habitats with groundwater.

CONCLUSIONS

Geomorphic gradients of landforms and associated catenas of soils in the Central Desert of

Baja California produce predictable and repeated patterns of plant community distribution. While there is dominance in coverage by a diverse group of relatively short-lived drought deciduous shrubs, this cover can vary greatly between years. Long-lived evergreen shrubs, non-CAM stem succulents and CAM succulents provide large proportions of aboveground biomass and water mass, with buffering and much less interannual fluctuations in these components.

The changing relative dominance of individual plant functional groups across these gradients of desert landforms reflects the morphological, phonological, and ecophysiological traits associated with each plant functional group. These traits strongly impact the relative importance of each functional group and thus the assembly rules of community composition (Weiher and Keddy 2001). Much more research is needed to better understand these assembly rules for arid ecosystems. Contrary to logical expectations, experimental studies with *Pachycereus pringlei* have suggested high that dense stands of seedlings may facilitate survival by reducing evaporative water losses from the soil surface (Bacilio et al. 2011). There is clearly much to learn about how plant facilitation networks are structures and how they may influence competition and species extinctions in desert habitats (Verdú and Valiente-Banuet 2008; Verdú et al. 2010).

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